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PROSTRATE GROWTH IN CAULESCENT ANDEAN ROSETTES OF *COESPELETIA* (ASTERACEAE, HELIANTHEAE)

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ABSTRACT

This note reports on the prostrate growth of caulescent Andean rosettes (*Coespeletia timotensis* Cuatr.) in the Venezuelan Andes. These plants normally grow erect and have a stem up to 3.5 m tall, but they can be tilted and toppled by frequent soil cryoturbation. Prostrate individuals tend to die as a result of toppling, but some can survive and continue growing in a decumbent position for a long time.

KEY WORDS: *Coespeletia timotensis*, Espeletiinae, Asteraceae, Heliantheae, stem morphology, páramo, Andes, Venezuela

INTRODUCTION

The north Andean páramos are commonly dominated by "giant" caulescent rosettes of *Espeletia* and related genera (subtribe Espeletiinae, Cuatrecasas 1976). In Venezuela, many high páramos are occupied by dense stands of *Coespeletia timotensis* Cuatr., which are found up to 4600 m (Pérez 1987a). Superficial soil movement due to recurrent frost activity can be a significant disturbance factor in the high páramo, both preventing the establishment of rosette seedlings and increasing the risk of adult mortality. Tall rosettes–up to 3.5 m–of *C. timotensis* seem to be easily destabilized by soil movement because their root systems are shallow, usually $\leq$ 25-30 cm (Monasterio 1980; Pérez 1987b). Soil cryoturbation commonly results in progressive tilting of the larger individuals, which eventually become completely prostrate on the soil surface and then die (Goldstein, *et al.* 1985). Some plants may escape this fate by germinating next to large rocks embedded in the ground, which can provide a stable anchorage (Pérez 1987b). Tilting of caulescent rosette plants also occurs in similar Afroalpine areas (Mahaney 1980; Beck, *et al.* 1983).

SURVIVAL OF TOPPLED ROSETTES

In the Páramo de Piedras Blancas (Venezuela), I have often found large toppled rosettes lying dead on the ground; in most cases, dead stems are concentrated in a few stands (cf. Monasterio 1980). These high mortality stands are more common on steep slopes and at higher elevations, where soil instability and frost activity are presumably greater. However, prostrate rosettes are not always dead, and I have found several examples of large, decumbent, living plants.

Figure 1 shows a recently toppled plant, about 180 cm long, lying on an 18° slope at 4470 m. Several dead stems were present in the vicinity, and the prostrate rosette itself was flanked by the remains of two dead plants. When visited, the slope was completely covered by striated soils, nubbins, and nonsorted stripes (Schubert 1975; Pérez 1987c); all are signs of recent needle ice activity, which is widespread in this páramo. The leaf crown of the decumbent rosette had phototropically tilted upwards about 35°; the plant showed no signs of senescence and seemed to be growing vigorously. Near this plant there were several more live fallen rosettes. One of them (Figure 2) showed a sharp, about 90° inflection along its stem, which grew horizontally for 130 cm and then vertically for 95 cm more (crown included). The roots of both rosettes were partially broken as a result of toppling, but clearly maintained enough of a connection with the soil to allow for continuous growth. In both cases, the plants were attached to the ground only at the stem base, and the trunks could be easily pulled and gently swung sideways; thus, no adventitious roots had been produced. This was expected, since *Coespeletia timotensis* appears to lack the capacity for vegetative reproduction (Monasterio 1980; Pérez 1987b).

A nearby group of live, prostrate plants was also examined at 4450 m. The slope here is steeper, about 26°, and has repeatedly shown, for the past eleven years, widespread evidence of needle ice growth, miniature debris flows, and superficial solifluction, which produces small "mud grooves" (Hastenrath 1973, 1989, pers. comm.). Measurements of needle ice activity on this slope for nearly six years (Pérez 1987c) indicate that a shallow soil layer $\leq$ 10 cm thick moves rapidly downhill, at rates of up to 15-18 cm/year. One decumbent rosette had a stem inflection of > 70°; the horizontal section near the ground was 140 cm long, the vertical one 105 cm (Figure 3). Fine debris, stones, and pieces of dead stems were piled upslope from the prostrate stem, where the ground stood up to 20 cm higher than on its downhill side. This attests again to the intensity of soil disturbance on this steep slope.

The morphological adaptations discussed here are by no means unique to *Coespeletia timotensis* or to Piedras Blancas. Although no similar reports have been found in the literature, Cuatrecasas (1990, pers. comm.) has occasionally seen decumbent Espeletiinae rosette plants with their leaf crowns erect and in

Figure 1 (above). Prostrate, recently toppled *Coespeletia timotensis* at 4470 m; the plant is 180 cm long. Note several dead rosettes in the background, and the leaning trunk of a large plant on the right side of the picture. Jan. 1990.

Figure 2 (below). Rosette specimen with sharply inflected stem, on same general location as that of Figure 1. The measuring stick is 180 cm long. Note two dead plant stems in the background, and the nubbin texture covering the soil surface. Jan. 1990.

Figure 3. Decumbent *Coespeletia timotensis* at 4450 m. The horizontal section is 140 cm long, the vertical one 105 cm. Note the piling of mineral and organic debris on the upslope side. Dec. 1985.

a vertical position after bending about 90° (cf. Figures 2, 3). He noticed this in a 1.2 + 0.3 m long (horizontal + vertical sections) specimen of *Espeletia arbelaezii* Cuatrecasas in the Páramo de Guantivá (Boyacá, Colombia), and also in a 1.0–1.2 m long *Ruilopezia figueirasii* (Cuatrecasas) Cuatrecasas (Cuatrecasas 1987) in the upper Andean forest of Sierra Santo Domingo (Venezuela). Cuatrecasas' observations agree with mine in that prostrate individuals with sharp stem inflections are always much scarcer than toppled, living plants lying on the ground with an unmodified stem (*i.e.*, Figure 1). This indicates that most rosettes probably do not survive toppling, and that only a few continue growing afterwards.

DISCUSSION AND CONCLUSIONS

The tilting model of Goldstein, *et al.* (1985) proposes that adult rosettes become gradually tilted until they are eventually prostrate on the soil surface. The examples presented here indicate that this is not always true. The sharp stem inflections observed in some surviving prostrate plants suggest that toppling was a rapid, discrete event. This may well have taken place following a period of progressive tilting, after which thresholds of root strength and/or soil stability were surpassed. The large, heavy rosettes fell to the ground suddenly, and the apical bud of those which survived became reoriented through negative geotropism and phototropic response, producing bent trunks afterwards. Sharp stem deflections would not be expected if tilting had always been gradual; a progressive curving of the stem should probably result instead. Further field observations support this hypothesis. In September 1980, a 230 cm tall rosette only 3 m away from that shown in Figure 3 was leaning slightly (ca. 25°) from the vertical. When the slope was revisited 17 months later (February 1982), this plant was found prostrate on the ground with its leaf crown tilted upwards ca. 45° (cf. Figure 1). Thus, the rosette toppled completely in a period of 1.5 years, at most. However, this plant did not survive the disturbance event; when the slope was revisited in 1990, the prostrate stem was dead, having become detached from the ground and rolled downslope a few meters.

The observations reported here show that toppling is not necessarily followed immediately by plant death. *Coespeletia timotensis* grows at about 15 mm/year (Smith 1974), thus, the largest prostrate individuals with bent stems continued growing for 50 to 70 years after toppling. Goldstein, *et al.* (1985) argue that death of fallen rosettes would occur due to root exposure and partial breakage, and the consequent drop in water and nutrient uptake. Also, the water storing pith tissue inside the stem would experience lower temperatures at the ground surface. Assuming not all the roots are irreparably damaged, several effects could counterbalance the exposure of the stem pith to the lower temperatures at the soil surface. First, the stem would be insulated from freezing along its underside; second, gradual piling of debris on the uphill side of plants falling perpendicular to the slope would partially bury the stem, further contributing to insulating it (Figure 3) (cf. Pérez 1987c, photo 2). In addition, if several plants topple synchronously, the stems at the edges of the fallen group may help insulate the prostrate plants at the center (Figure 1), further minimizing their exposure to extreme cold at least until the dead stems decompose.

It must be pointed out that the assumption that soil cryoturbation is the sole cause of rosette toppling is simplistic. Although frost induced creep and gelifluction are certainly significant geomorphic agents in this páramo, many other processes, including debris- and mudflows, surface runoff, throughflow, dry grain flows, rockfalls, and cattle disturbance can affect substrate stability (Pérez 1987b, 1987c) and thus cause plant tilting and toppling. Survival and continued growth of prostrate caulescent rosettes in the periglacial páramo occurs only occasionally, but merits attention as a significant morphological adaptation which partially counteracts the noxious effects of ground disturbance on the tallest plants.

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